The effect of age on visuomotor learning processes

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Abstract

People can rapidly adapt their movements to a wide array of changes in our environment or the motor apparatus, although this ability can decline with age. Adaptation of movements, such as reaching with altered visual feedback, is thought to rely on the quality of sensory feedback and how well we can predict our movements. Cognitive strategies can also contribute to how quickly adaptation can occur. Age-related declines in sensory acuity and cognitive function, such as strategy use, may explain poorer adaptation in older adults compared to younger adults. The current study tested the effects of instruction and strategy use on how well older (n=38) and younger (n=42) adults were able to compensate for a 30° visuomotor rotation during reach-training, and use this strategy afterwards when reaching without a cursor. Next, training-induced changes in proprioceptive and predicted estimates of the adapted hand in these two age groups were compared. This was done by having older and younger adults estimate the location of their unseen hand when it was either moved out by a robot (passive localization: proprioception only, no prediction) or was moved by the participant themselves (active localization: prediction and proprioception) before and after visuomotor adaptation. The difference between these localization tasks represents changes in predicted or efferent-based estimates. Instruction benefitted older adults' less than younger adults during initial reach training, but a similar pattern in reach aftereffects in the two age groups suggests that older adults' strategy use could be evoked during no-cursor reaches after sufficient training. Following visuomotor adaptation, older adults, whether instructed or not, showed larger visually driven changes in their passive or proprioceptive hand estimates but not their efferent-based or predicted estimates of hand position. These results suggest that older adults do not differ much from younger adults in their ability to adapt their reaching movements implicitly or use cognitive strategies; however their estimates of updated hand proprioception are more affected by visual training.

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Introduction

Our brains have evolved to adapt our movements to changing situations, including those in our bodies, such as muscle strength, and those in the environment, such as working with new tools. Indeed, our capacity to learn new movements and adapt them to different circumstances renders us versatile movers. However, in some cases, our ability to adapt our movements is diminished with age (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2011; Bock & Girgenrath, 2006; Buch, E. R.; Young, S.; Contreras-Vidal, 2003; Fernández-Ruiz, Hall, Vergara, & Díaz, 2000; Hegele & Heuer, 2013; Heuer & Hegele, 2008; Seidler, 2006); it is unclear why. Some contributing factors could be a decreased ability to use cognitive control, such as using a conscious strategy, when adapting movements to altered circumstances (Hegele & Heuer, 2013; Heuer & Hegele, 2008) and/or declining sensory acuity with age. Sensory feedback on the position of objects in space and our limbs is critical in controlling and adapting movements. If the quality of this feedback diminishes with age, less accurate and precise motor control may result, hence leading to dampened motor learning.

Training with altered visual feedback of the hand leads to motor adaptation in younger adults and as a consequence can change younger adults' estimates of limb position. If these estimates are considered both less accurate and precise in older adults, they should change more in motor learning. The goals of this study are to compare in older and younger adults, the effect of the use of task instruction in motor learning, and the effect of this visuomotor learning on both sensory estimates and efferent-based estimates of hand location. Understanding how the role of cognitive and sensory processes in motor learning change with age can have important implications for training and rehabilitation to overcome or compensate for age-related sensory and motor deficits.

Visuomotor Adaptation: Measuring Motor learning

The visuomotor adaptation paradigm is commonly used for studying motor learning; in this paradigm, participants repeatedly reach for a target when the viewed position of their hand is altered. Rapidly over trials, peoples' reaching adapts to the visual inputs. Adapting our reaching movements involve adjusting a well-learned behavior in response to a systematic perturbation (Cunningham, 1989). Compared to learning a new movement or skill (skill acquisition), adaptation occurs quickly and thus provides a way to measure motor learning. One of the most common ways of altering visual feedback of the hand involves participants reaching with a cursor that represents their hand, and manipulating the direction of cursor motion relative to actual hand motion with respect to a common start position (Krakauer, Pine, Ghilardi, & Ghez, 2000), either in the clockwise (CW) or counter-clockwise (CCW) direction (Figure 1). The reach adaptation paradigm is a quick and easy method to measure motor learning, and therefore it is a useful way to investigate how motor learning is affected by aging.

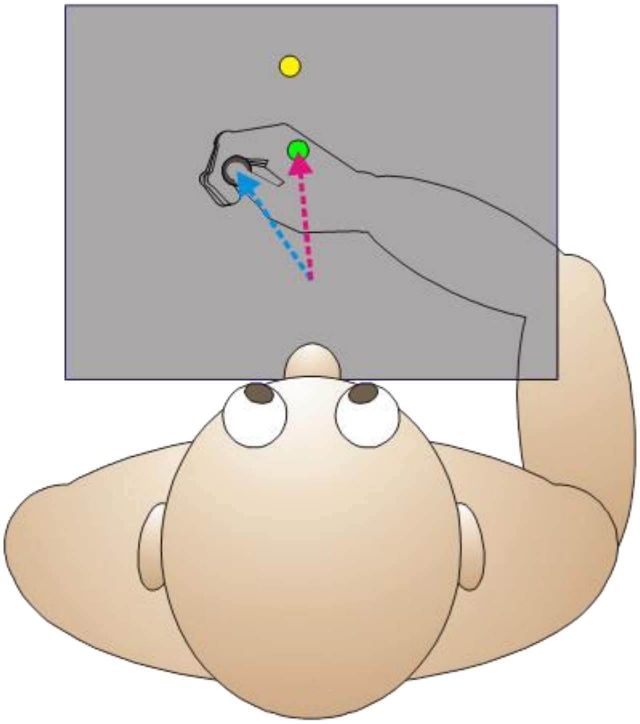


Figure 1: Demonstration of a reach movement (Dashed dark pink line) made with a rotated cursor (Green circle) to a diagonal target (Yellow circle). The hand (here shown) is actually hidden from participants; its path is shown as a blue dashed line. In this example, the cursor is rotated 30 ° CW relative to start position.

When initially reaching with this misaligned cursor, the participant produces large directional errors in initial reaching direction that quickly decrease with further training after the first few trials. This improvement slows down until there is minimal error in reach performance. When trying to reach to a single target, people take on average only 20 trials to adapt to a 30° cursor rotation, and approximately 60 trials when reaching to multiple targets presented sequentially (Krakauer et al., 2000; Neva & Henriques, 2013). Thus, people learn quickly to adjust their hand movement in order to move the cursor directly to the target. Even after the visual perturbation is removed, this deviation in hand movements continues for a short time. This persistence in the adapted hand movements is known as an aftereffect and represents a measure of implicit learning. Here, reach aftereffects is used to study motor learning.

The Effect of Explicit Awareness on Motor Learning

Unsurprisingly, being aware of the cursor manipulation alters the motor learning rate. Instructing participants about how to compensate for the visual perturbation usually leads to smaller errors in initial reaching trials (Benson, Anguera, & Seidler, 2011; Bond & Taylor, 2015; Hegele & Heuer, 2013; Heuer & Hegele, 2008; Heuer, Hegele, & Sülzenbrück, 2011; Mazzoni & Krakauer, 2006; Werner et al., 2015). For example, to instruct participants where to actually direct their hand to get the cursor on the target, Mazzoni and Krakauer (2006) showed landmarks next to the targets; Benson, Anguera, and Seidler (2011) used a clock face to illustrate the 30° rotation necessary for the cursor to reach the target. In the latter study, those who were given instructions showed significantly smaller directional errors (roughly 33% of the 30° rotation) than those who were not informed (roughly full 30° rotation). This advantage was apparent in the first few training trials. After about 40 trials, there was no difference between the two groups. Using an equivalent clock demonstration, Werner et al. (2015) found a similar advantage in early learning rate for participants given instructions compared to those who were not, when adapting to multiple cursor rotations. Specifically, instructed participants compensated for almost half of the rotation in the first few trials for a 20° rotation and about 25% for the 60° rotation. In contrast, Taylor et al. (2014) found only a small benefit for initial learning for those given instructions to aim at a target compared to those who were not. That is, the initial hand movements were compensating for about 10% of the 45° rotation within the first block of trials. Nonetheless, despite Taylor et al. (2014)'s instructions not benefitting participants to the same extent as Werner et al. (2015), instruction usually does lead to benefits in learning (greater compensation) at the beginning of training.

Despite not finding a huge effect of instruction on motor learning, Taylor et al. (2014) suggest that initial adaptation largely reflects explicit learning. They measured this explicit component by having participants verbally report their aiming direction prior to every reach-training trial with a 45° cursor rotation. Using this aiming strategy, they deduced the time-course of explicit and implicit (by subtracting the explicit) contributions to visuomotor adaptation. Thus, this ”implicit” change refers to the difference between the direction the hand actually moved with the rotated-cursor and the direction that people explicitly report they were going to move. They found that the explicit contribution was large and rapid during initial training, peaking within ten trials, but gradually reduced with further training, where the implicit process contributed more substantially. This implicit component is thought to arise when updating the visuomotor mapping (also sometimes referred to as modifying or updating an internal model) driven by sensorimotor prediction errors. The size of the reach aftereffects (produced without cursor) was similar to that of the implicit contribution during final training trials. Using the same aiming strategy, the extent and pattern of the explicit and implicit contributions remained largely the same for different rotation sizes and different number of targets (Bond & Taylor, 2015). In fact, Bond and Taylor (2015) found that the slope and extent (roughly 12°) of the implicit component was similar across cursor-rotations that ranged from 15 to 90°. This finding suggests that either a larger conspicuous rotation elicit more explicit learning and/or implicit learning is robust against rotation size. However, this attempt to measure the explicit component, that is the strategy that the participant was using, may have also influenced performance by making the participant more aware of the visuomotor rotation. While explicit processes likely dominate at early stages of learning, the extent of the contribution of implicit and explicit processes, and how this changes with aging, is still unclear.

Werner et al. (2015) addressed the problem of dissociating explicit and implicit processes by measuring awareness using a post-training test known as a process dissociation procedure (PDP). The PDP consisted of asking participants to apply or not apply any strategies that were used during training with a visual perturbation when reaching without any visual feedback (cursor is invisible). Those who were told how to counter the cursor-rotation or who became aware of the nature of the perturbation in another way were able to evoke the strategy when asked; thus producing larger hand deviations compared to when not applying the strategy. This way of assessing awareness does not have the same pitfalls as in prior studies, and we will use the PDP approach to assess both older and younger adults' awareness of the nature of the perturbation.

Prediction and Proprioception following Visuomotor Adaptation

Not only do instructions play an important role in motor learning, but so does the quality of sensory feedback (both proprioceptive and visual) as well as efferent-based estimates of limb location. Efferent-based estimates are assumed to be important in adapting volitional (self-generated) movement. Before we make a reaching movement, we have an efferent-based copy of the motor command that can be used to predict the subsequent hand movement using forward computation or a forward model. This can be combined with sensory feedback from the actual hand movement (Figure 2). Together they contribute to estimates of hand position and motion necessary for motor control and learning.

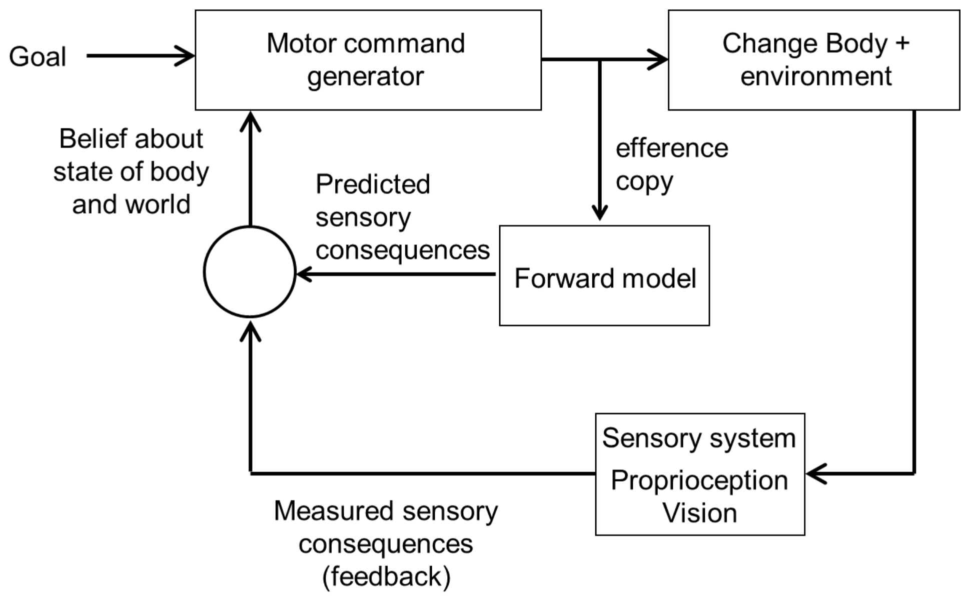


Figure 2: Optimal feedback Control Model. After a movement goal has been selected (Goal top left corner), a motor command (i.e. change in the body and/or the environment) is generated which produces a movement (Motor command generator box). Prior to and during the movement, a copy of the motor command —the efference copy, is generated and used by various brain areas to estimate or predict the ongoing consequences of the movement, known theoretically as a forward model. This is combined with sensory feedback available during the movement.

Visuomotor adaptation consistently changes people's proprioceptive estimate of hand position, in a process called proprioceptive recalibration (Barkley, Salomonczyk, Cressman, & Henriques, 2014; Cameron, Franks, Inglis, & Chua, 2012; Clayton, Cressman, & Henriques, 2014; Cressman & Henriques, 2009; Cressman, Salomonczyk, & Henriques, 2010; Marius 't Hart & Henriques, 2016; Mostafa, Kamran-disfani, Bahari-kashani, Cressman, & Henriques, 2015; Ruttle, Cressman, Marius 't Hart, & Henriques, 2016). This recalibration is usually about 20% of the size of visual distortion and it occurs only for the trained hand (Cameron et al., 2012; Mostafa et al., 2015). It arises for different rotation sizes (Salomonczyk, Cressman, & Henriques, 2011) and for different types of feedback, such as visual feedback at the end of the reach and continuous cursor feedback (Barkley et al., 2014). This recalibration of hand proprioception following visuomotor learning occurs for various methods of measuring proprioception(Clayton et al., 2014; Cressman & Henriques, 2010). It occurs for young and older adults and people with mild cerebellar damage (Cressman et al., 2010; Henriques, Filippopulos, Straube, & Eggert, 2014) It is also present following force field adaptation(e.g. Ostry, Darainy, Mattar, Wong, & Gribble, 2010). This effect is robust and appears as an important aspect for motor learning. In all these proprioceptive tasks in the studies above, the trained hand was always passively moved or constrained in order to isolate changes in proprioception from motor changes.

Other studies have attempted to investigate changes in the efferent-based or predicted estimate of hand motion following visuomotor learning. They did so by having participants generate their own hand movements during proprioceptive tasks (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012; Synofzik, Lindner, & Thier, 2008). With such self-generated unseen movements, not only would proprioception be available, but a copy of the motor command would also be. As illustrated in Figure 2, using these efferent signals in forward computations (or a forward model), the brain can "predict" the upcoming motion of the hand prior to the availability of sensory feedback (Colby, Duhamel, & Goldberg, 1995). The cerebellum is considered responsible for the majority of these forward computations (Ebner & Pasalar, 2008). To examine how these predicted estimates of hand motion change, Izawa et al. (2012) measured the predicted estimates of hand motion during a task self-generated motion in healthy adults and patients with cerebellum damage after adapting to a visuomotor rotation. They found that changes in estimates of the unseen hand motion were larger in healthy participants compared to patients, and concluded that shifts in hand localization are mainly driven by changes in predicted estimates. However, these shifts may not only be due to a change in predictions, given that proprioception also changes following visuomotor learning and these changes appear to occur even in cerebellar patients (Henriques et al., 2014).

A method that allows us to disentangle the extent that these shifts in hand localization following visuomotor learning are due to changes in prediction as opposed to changes in proprioception has been developed by 't Hart and Henriques (2016). They compared the differences in hand localization both when the hand movement was self-generated (as in Izawa et al. 2014) and when it was passively displaced by a robot. As mentioned above, estimates of the self-generated hand movements are based both on proprioceptive feedback and efferent-based estimates; while passive movement is only based on proprioceptive feedback (this passive displacement produces no efferent signal). In both types of hand displacement, visuomotor adaptation led to significant shifts in localization estimates (shifts due to self-generated hand movements were slightly larger than those due proprioception). This suggests that through learning, changes in hand localization may mainly be due to proprioceptive recalibration.

Age-related changes in Proprioception

Many studies have shown that by using a variety of proprioceptive acuity tasks, older adults are less precise in estimating their own unseen limb position or joint angles compared to young adults (as reviewed by Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009). Cressman et al. (2010) also showed that older adults showed on average 25% larger uncertainty range (just noticeable difference) in estimating the location of the unseen hand (with reference to a landmark), compared to that of younger adults. However, the accuracy was equivalent in the two age groups. Lei and Wang (2017) also found that compared to younger adults, older adults showed on average larger variability in estimates of the joint position of either arm when passively moved. Note that for the most part, older adults are less precise when estimating limb positions.

Since proprioception plays a role in motor learning and its precision declines with age, decreased proprioceptive acuity may be related to a decline in motor learning with age. There is some evidence that the larger variability in estimates of hand location is associated with a poorer rate of adaptation for older adults, but not for young adults (Lei & Wang, 2017). Cressman et al. (2010) however, found no differences in reach aftereffects following adaptation to a gradually introduced rotation between older and younger adults, despite age-related differences in proprioceptive acuity. It is possible that poorer proprioceptive acuity affects the rate of visuomotor learning, but not its subsequent aftereffect. Although there is evidence that people with sensory neuropathy (i.e. no spindle-based proprioception) can adapt to a rotated cursor, suggesting that proprioception is likely important, but it may not be critical for adaptation. Conversely, it may be that visuomotor learning leads to larger changes in proprioceptive estimates of hand position in people with poorer proprioceptive acuity, like older adults. Whether the proprioceptive recalibration is larger in older adults is assessed here.

Although there is a lot of evidence that proprioceptive feedback/acuity diminishes with age (Goble et al., 2012, 2009; Rand, Wang, Müsseler, & Heuer, 2013; Wolpe et al., 2016), there are no studies that suggest age-related differences in people's efferent-based estimates of hand motion. This is partly because there are few studies that have been able to isolate estimates of hand based on efferent-signals and forward computations alone (since proprioceptive feedback is always available). And none of these studies have investigated this across age groups. There is one study that suggests indirectly that older adults may not show deficits in efferent-based estimates. In fact, Moran, Symmonds, Dolan, and Friston, (2014) suggest that with age comes more experiences and adaptation to the environment, thus brain functions become highly specialized. Based on a lifetime of moving and interacting with the environment, forward models used to simulate and represent the body and environments may not deteriorate like sensory inputs, or at least not to the same extent. Signals for estimating body motion may highly rely on extensive sensory experience in life. This advantage may help overcome the noisier proprioceptive acuity with age.

Recent work by Wolpe and colleagues (2016) support the hypothesis that older adults rely on predictions from prior sensory experience in life in light of degrading sensory feedback. Indeed, their results suggest that the intensity of afferent sensory signals on self-generated movements (movements with an efferent copy of the motor command) may be attenuated with age in proportion to reduced sensory sensitivity. In this study, when younger and older adults performed a force-matching task by reproducing with their right index finger a force that was applied to their left index finger, older adults tended to overcompensate by producing a consistently larger force, despite being accurate when estimates were indirect. Wolpe et al. (2016) interpreted the over-estimation of force in the direct condition as older adults downplaying the sensory feedback while emphasizing predictions. These results illustrate how age-related increases in sensory noise may lead to greater reliance on efference signals to compensate for changes in motor control. Thus, it is possible that when localizing the hand or body, older adults may rely more on the predicted sensory consequences of a movement over noisy proprioceptive feedback. However, questions remain about the extent that older adults rely on both the predicted and actual sensory feedback when adapting their reaching movements to a visuomotor rotation and how (imprecise) proprioceptive feedback from their hand contribute to their ability to adapt.

Thus, while there is a large literature suggesting that proprioception declines with age, and some evidence that suggest that this decline might contribute to motor learning, there does not appear to be any evidence to suggest that older adults show differences in efferent-based estimation of limb position or motion. This thesis investigates this question indirectly, and serves as a basis for future studies that directly compare afferent and efferent-based proprioception and whether poorer proprioceptive acuity (poorer precision) explains differences in visuomotor adaptation and proprioceptive recalibration.

Age-related changes affect Visuomotor Adaptation

Similarly to younger adults, older adults (50 years plus) are able to adapt their reaches to a visuomotor rotation of the hand, but in some cases to a lesser extent (slower or less complete learning) compared to younger adults. Specifically, when adapting to large cursor rotations (60 or 90°), older adults do not adapt at the same rate nor to the same extent as younger adults (Anguera et al., 2011; Bock & Girgenrath, 2006; Buch, E. R.; Young, S.; Contreras-Vidal, 2003; Fernández-Ruiz et al., 2000; Heuer & Hegele, 2008; Heuer et al., 2011; King, Fogel, Albouy, & Doyon, 2013; Seidler, 2006). For example, Buch, Young, and Contreras-Vidal (2003) found older adults needed more reach training trials to adapt to the same extent as younger adults when exposed to an abrupt 90 degree visuomotor rotation, but there were no age-related differences when adapting to a gradual visuomotor rotation. Similar to gradual rotations, adapting to smaller rotations (30 or 45°) do not lead to differences in the rate of learning of younger and older adults (Heuer & Hegele, 2008; Seidler, 2006). However, this is not always the case; Lei and Wang (2017) found that the adaptation rate (the speed of change) of older adults was only two-thirds as fast as those of younger adults. Despite differences in the adaptation rate following training with larger visuomotor rotations, older adults tend to produce similar or even larger reach aftereffects than young adults (Anguera et al., 2011; Bock & Girgenrath, 2006; Buch, , Young, & Contreras-Vidal, 2003; Cressman et al., 2010; Fernández-Ruiz et al., 2000; Hegele & Heuer, 2010; Heuer &

Hegele, 2008; Seidler, 2006). As mentioned above, reach aftereffects reflect an implicit component of learning. This also suggests that what drives the differences in motor learning between older and younger adults might be largely due to changes in explicit processes rather than implicit.

A possible explanation for age-related differences in the initial learning for larger rotations, less consistent differences for smaller rotations, and similar reach aftereffects in all cases, may be that older adults might not be able to maximize and/or figure out explicit strategies. Because larger rotations produce larger initial reaching errors than smaller rotations, they are more likely to require and evoke cognitive processes (explicit processes), such as those associated with strategy use, to compensate for the rotation. This is in contrast to smaller rotations where reaching errors are smaller and thus does not evoke the same cognitive processes (implicit processes). As described, Werner et al (2016) showed that in young adults, training with small rotations usually do not elicit strategies, although training with larger rotations do. It could be that, during the earlier stages of learning, older adults have problems developing and applying these intentional changes or strategies. In other words, age-related differences in adaptation may have to do with differences in the explicit component of learning, while the implicit component remains largely invariable with age.

This hypothesis is somewhat supported by the work of Heuer and Hegele (2008, 2011, 2013). They measured intentional changes by having people verbally indicate the extent by which their hand movement had to be deviated in order to compensate for a 75° rotated cursor, following training with the same distortion. Older adults were less likely to verbally indicate such changes. When they did, they underestimated the angles needed to reach to the target with the perturbation. They also had participants perform reach trials where there was no-cursor representing their hand position, both when told to use the strategy (cued-rotation) and when not (reach aftereffect cued no-rotation) similar to Werner et al. (2015). For both age groups, reach aftereffects were larger when told to use the strategy than when not. This serves as evidence that participants did develop and applied a strategy. There was no difference in the reach aftereffect (cued no-rotation) between the two age groups, but older adults did not have as large of a change in the reaches that required using a strategy; that is, when reaching without a cursor but with cued-rotation, the older adults demonstrated less adjustment. These age-related differences persisted even for another group who were both told about the distortion and given feedback regarding the accuracy of their verbal reports (Heuer & Hegele, 2013). However, when a 30° rotation was used, Heuer and Hegele (2008) did not find differences in no-cursor reaches with cued rotation. Age-related differences in adaptation to large visuomotor distortions may be due to less initiation and/or use of explicit strategies in older adults.

Age-related changes in Neural Networks associated with Cognition affect Motor Learning

In some instances, age-related deficiencies in motor adaptation can be partially explained by changes in neural networks associated with cognition (Park et al., 2002). This could underlie the failure of older adults to engage in explicit cognitive strategies to reduce errors in reaching and thus result in poor learning rates (Anguera et al., 2012; Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010). Spatial working memory (SWM) is an important predictor of the initial adaptation rate to a visuomotor rotation (Anguera et al., 2012). For example, in younger adults, Anguera, Reuter-Lorenz, Willingham, and Seidler (2010) found that poorer SWM correlates with poorer initial adaptation to a 30° counter clockwise (CCW) visuomotor rotation. Consistently, they found overlapping brain region activity patterns when initially adapting to a visuomotor rotation and doing a mental rotation task. This suggests that the same brain regions are involved in some SWM tasks, such as the mental card rotation task, and in adaptation to visuomotor rotation. In older adults, no such correlation between behavioral and imaging measures was found (Anguera et al., 2011). They suggest that brain processing involved in SWM may be also responsible for accurate reaching with a rotation.

Hypotheses. In light of their age-related decreases in working memory and spatial ability (Anguera et al., 2010, 2011; Craik & Grady, 2009), older adults may not able to benefit from or develop explicit strategies during motor learning to the same extent as younger adults. This was tested by giving an explicit strategy, via verbal instructions on how to compensate for the visuomotor rotation. Next, the effect of instructions on initial motor learning in older adults was compared with younger adults. If age affects the ability to use strategies to adapt to a cursor rotation, compared to younger adults, older adults should reduce their rotation cursor-errors to a lesser extent during initial training. If older adults benefit at all from instruction, then they should show a large reduction in initial reaching errors compared to non-instructed old adults. Reach aftereffects (no-cursor reaches) produced when told to use or not use a strategy (PDP discussed previously) are compared. This difference is a measure of the explicit contribution, or awareness of the nature of the perturbation, in reach adaptation. Then how these differences in reach aftereffects change with age is evaluated.

The second hypothesis is that given age-related differences in proprioceptive acuity, it is possible that visually-induced learning will lead to greater changes in proprioceptive estimates (i.e., proprioceptive recalibration) in older adults compared to younger adults. It is unclear whether similar training induced changes in efferent-based estimates of hand motion will differ as a function of age.

Overall, this project investigates how age-related cognitive and sensory decline may affect motor adaptation. It enables a more comprehensive understanding of the interaction between different causes of age-related changes in motor performance.

Methods

Participants

Forty-two young (Age: M = 20.93, SD = 2.77) and thirty-eight older (Age: M = 70.05, SD = 6.78) adults were recruited through various research participant pool at York University: the Undergraduate Research Participant Pool (URPP), Kinesiology Undergraduate Research Participant Pool (KURE), and York Research Participant Pool (YRPP), and outside the university from the Driftwood community centre. All participants had normal or corrected-to-normal visual acuity, were right handed, and self-reported that they were in good health and were able to understand the tasks. Participants were asked to give their informed written consent before taking part in the study (Appendix D). The participants from the undergraduate research pools were given course credit towards either their PSCY 1010 or KINE 2049 course for participation. Older adults who were recruited through the YRPP or the community centre were paid an honorarium and lunch, as required by the YRPP to compensate for time and travel to the university. The York Human Participants Review Sub-committee approved this study.

Apparatus

The apparatus is shown in Figure 3. Participants were seated at a table on a height-adjustable chair so that they could comfortably see and reach to displayed targets projected from a monitor (Samsung 510 N, 60 Hz), located 17 cm above a 2-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA). The chair was fixed in its position for the duration of the experiment. Participants were asked to grip a vertical handle with their right hand. They were instructed to place their right thumb on a screw located on top of the robot handle. The handle was attached to the free end of the robot manipulandum and could be moved on a horizontal plane. A thick black cloth was draped and tucked over participants' right shoulder to ensure that they did not see their right arm. See Figure 3 A.

A downward-facing computer monitor was mounted above a reflective surface located approximately 10 cm between the surface of the monitor and the surface above the robot manipulandum. Consequently, the reflection of the cursor and the targets appeared on the same plane as the thumb of the right hand. The reflective surface also occluded the hand and arm. Before each trial, the name of the task was shown on the reflective screen. During reach training trials, participants' hand position was represented as a cursor (1.0 cm in diameter) and its color changed according to its position relative to the hand; it became green if it was aligned or blue if misaligned (rotated). The targets were yellow dots (1.0 cm in diameter) located 10 cm away either straight in front of the home position or at a 45° angle clockwise (CW) and counter clockwise (CCW) from the forward target (the targets are shown as yellow circles and home position, as a red circle in Figure 3B). At the beginning of each trial, the hand is locked into place at home position located 20 cm in front of the body midline.

During some tasks, participants used their visible left hand (illuminated by a lamp above the touchscreen) to press on a touchscreen panel placed horizontally just above the robot-handle (Keytec Inc., Garland, TX, USA with a resolution of 205 × 205 pixels located ~3.5 cm above the thumb) to indicate the perceived position of their unseen right thumb (Figure 3A and C).

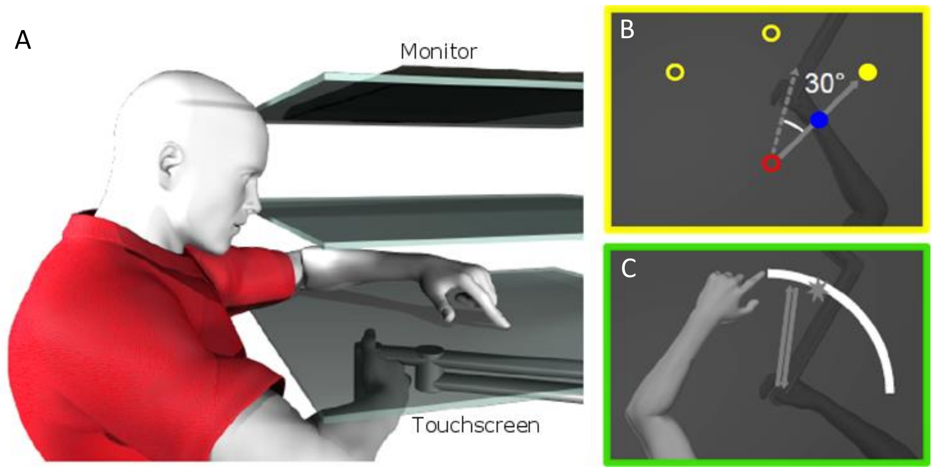


Figure 3. Apparatus and experimental setup. A: Participants moved their right hand while gripping the handle of a two-joint robot manipulandum. Stimuli are produced by a monitor face-down (top surface) above a reflective surface (middle). The touchscreen panel is located below the reflective surface and just above the robot handle (bottom). B: Training task: The three yellow circles represent the targets. They can either be directly in front of the home position (illustrated as a red open circles), be 45° clockwise (CW) or counter clockwise (CCW) from it. During reach training, a visuomotor rotation was introduced: the cursor is blue and rotated 30° CW (solid vector) from the actual (unseen) hand position/direction (dashed vector) relative to the home position. C: Localization task: Using ’t Hart and Henriques (2016)’s localization task, the unseen right hand was moved to a location along a white arc either by participants voluntarily moving their hand or having their hand physically moved by the robot. Once the right hand returned to its home position, and participants indicated where the right hand had intersected the arc by touching the touchscreen location with their visible left hand.

Procedure

Two experimental sessions were conducted. Each session had the same four tasks (described in detail below) and the name of each task was displayed on the reflective surface every time prior to commencement. The first session (illustrated on the top row of Figure 4) measured baseline results (where training involved reaching with an aligned cursor). The second session (bottom row) involved training with a 30° CW rotated cursor. Reach training was followed by three additional tasks (illustrated by each column in Figure 4). Each set of four tasks was repeated four times, with the two sessions (Training with aligned cursor and rotation) separated by a break. During the break, half of the participants were instructed about the nature of this 30° perturbation while the other half was not. Participants took breaks as desired between each set of experimental sessions.

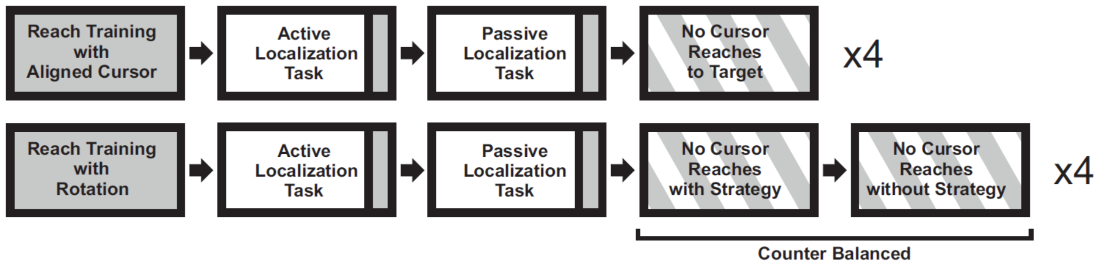


Figure 4. Task order for the two sessions (depicted in two rows). First session is the baseline session (top) where reach training involved an aligned-cursor and the second session involved training with a rotated cursor. Each session began with reach training and consisted of four tasks (e.g. reach training, active localization, passive localization, and no cursor reaches for one block of top row). Each set of four tasks represents a block, and each block was completed four times, starting with training (dark grey box) with either an aligned cursor (top) or a rotated cursor (bottom). This was followed by two hand localization tasks, during which participants moved their own unseen hand to the arc (Active localization, first white box) and then the robot guided their hand (Passive localization, second white box). "Top-up" reach training followed these localization tasks; it was included between each localization tasks (small grey box attached to Active and Passive localization box). Each block ended with the no-cursor reach tasks (Striped box). For those no-cursor reaches following training with a visuomotor rotation (bottom), participants were once told to not use their strategy (No Cursor Reaches without Strategy) and once to use it (No Cursor reaches with Strategy); half the participants started with the strategy and finished without, and vice-versa for the other half. These tasks were counterbalanced within and between participants.

Training. In the training tasks (Figure 3B, and solid grey boxes in Figure 4), prior to the task, the words "Reach To Target" were displayed, then participants reached to one of three visual targets. The target appeared at the beginning of a trial, and a cursor appeared 300 ms later, at which point participants hand can leave the home position. The target and cursor disappeared once the reach movement was complete, i.e. when the center of the hand cursor was positioned within 0.5 cm of the target's center. Afterwards, participants moved their hand back towards the home position along a constrained straight path [generated by a perpendicular resistance force of 2 N/(mm/s) and a viscous damping of 5 N/(mm/s)] to begin the next trial.

The first training task was the *Reach training with aligned cursor* (in Session 1, first box in the top row of Figure 4). During this training, the cursor was aligned with the hand position; it included 60 trials, and nine “top-up” trials (grey boxes in Figure 4) followed each hand localization task (Appendix G for break-down of trials). The second training task was *the Reach training with rotated cursor* (in Session 2, first box in the bottom row of Figure 4). In this training, the cursor was rotated by 30º CW around the home position; it included 90 trials and an additional 30 “top-up” trials.

Instructions. For both the older and younger adult groups, half of the participants were instructed on a strategy to counteract a 30º CW perturbation, and the other half did not get this instruction. Instruction was provided using Powerpoint demonstration along with a verbal explanation (Appendix C) and a clock diagram (Appendix B). It was ensured that participants understood these instructions; i.e., that they could draw three arrows on a clock illustrating the direction at which they would reach when using this provided strategy. The non-instructed participants were told that the reach training tasks will be different as the cursor will not move the same way as it did previously, and they will need to compensate for it by figuring out an appropriate strategy. They were also told they would be called upon to use this strategy during some no-cursor reaches (described in detail below).

No-cursor reaches. Prior to the task, the words “No-Cursor” were displayed, then participants reached to the same three targets described above but without visual feedback about the position of their hand (cursor) (striped grey boxes in Figure 4); trials were considered complete when participants believed they had acquired the target by holding their hand still for at least 500 ms. Once the reach was completed, participants moved the robot handle back to the home position in order to begin the next one. During baseline (first session), the no-cursor reach tasks involved asking participants to reach to the target nine times in each four blocks (for a total of 36 trials). During training with the rotation cursor (second session), these no-cursor trials were split into two sub-tasks (of nine trials each). In one sub-task, participants viewed the words "No-Cursor with Strategy" displayed on the monitor, and were required to use the strategy that they developed during their recent training with the blue cursor. In the other subtask, participants saw the words "No-Cursor without Strategy" and they were asked to not use a compensatory strategy and reach as they did in the baseline reach-to-target task with the green cursor. [This procedure is based on the methods used by Werner et al. (2015) to assess the effects of awareness on motor learning (e.g. explicit and implicit learning).] The order of these subtasks was counterbalanced between each consecutive participant. Each pair of subtasks was repeated four times (for a total of 72 trials).

The results of the no-cursor reaches with and without the proposed strategy were compared, as per the process dissociation procedure (PDP) (used by Werner et al., 2015 and defined in the introduction), to determine the levels of explicit and implicit learning, respectively. This procedure was used to determine if participants were aware of the nature of the rotation and could apply the strategy when asked even if they had no visual feedback of their hand.

Localization tasks. The localization tasks assessed the participants' estimated location of their unseen hand following reach training when they generated their unseen hand movement themselves (Active hand-localization task) and when the robot displaced their hand (Passive hand-localization task) to the white arc (Figure 3C).

In the **Active hand-localization task** (first white boxes in Figure 4), the words "Active Localization" were displayed prior to each task, and participants made a quick and straight hand movement with the robot manipulandum toward and past a chosen point on a white arc located 10 cm away from the home position (Figure 4C). When the robot manipulandum reached the distance of the arc, a force "cushion" was applied to prevent the participant from moving their hand past the arc, giving them the sensation of hitting a soft wall. After "hitting the wall", participants' right hand returned to the home position (with robot-guidance as in the other tasks) and then used their visible left hand to indicate on the touch screen the point where the right hand intersected the arc (Figure 4A). To avoid confounding contact with the touch screen, participants placed their left hand under their chin between each response. Three arc spans were used (from 0° to 60°, 60° to 120°, and 120° to 180° in polar coordinates); and six hand localization trials were completed at each of these spans (for a total of 18 trials) for each of the four repetitions (Figure 2) for a total of 72 trials per session.

In the **Passive hand-localization task** (second white boxes in Figure 4), the words "Passive Localization" were displayed prior to each task, and participants' unseen right hand was pulled by the robot manipulandum to various points on the arc. These points were those actively chosen in the previous Active hand-localization task, but they were presented in a random order. Like in the Active hand-localization task, after the robot moved their unseen right hand to a point on the arc, their hand was guided back to the home position and they indicated with their visible left hand the location of the point on the arc where the right hand had been (Figure 4). This was done for the same number of trials as in the Active hand-localization task.

As summarized in Figure 4, all participants completed an ordered set of four tasks per session, first session with aligned-cursor training and second session with rotated-cursor training.

After completing both sessions of the experiment, participants were then asked a series of questions to assess awareness of the perturbation (Appendix A).

Measures

The performance during training (both with a rotated cursor and an aligned cursor), the reach errors in the no-cursor reach tasks that followed each training task, and the estimate of the visible left hand of the unseen right hand during the localization tasks are calculated. For reach performance during training, the initial direction of the hand movement in degrees is taken at peak velocity (in both aligned and rotations sessions); this is defined as reach directions. The differences in the reach directions in the second session (with rotated cursor) compared to the first (aligned cursor) session are known as reach deviations. For no-cursor reaches, the end-point hand angle in degrees is used to make them comparable to hand-position estimates in the localization tasks, and these are defined as no-cursor reach directions. The angular difference between no-cursor reach directions from the two sessions are referred to as no cursor reach deviations.

For the localization tasks, hand-position estimates refer to where participants indicate with their visible left hand (on the touchscreen) the angular location of their unseen right hand; this is done relative to the actual hand location on the arc in degrees. Since in the Active localization task, participants could volitionally choose a hand movement direction for their unseen right hand, and Passive localization tasks used the same final hand positions, hand movements in both localization tasks were not uniformly distributed across the workspace. Therefore, a kernel smoothing (normal kernel with a width of 7.5 degrees) at the same specified discrete points provided an interpolated estimate of what the localization response would be with the hand located at those points. This was done for every participant for both the aligned and rotated sessions.

For localization tasks, Passive localization estimates are known as Passive Hand-Estimates, whereas active hand-estimates for Active localization are known as Active Hand-Position Estimates. The differences in hand-position estimates between the two sessions are referred to as Localization Shifts, but more specifically those for the passive localization tasks will be called Proprioceptive Hand Shifts. The measure of predicted changes in localization is obtained by subtracting shifts in Active localization from those in Passive localization tasks, and is defined as an Updated Predicted Hand Shift.

Outlier Removal

The hand path and velocity profile of every single reach trial (with cursor or without) and the endpoint for every localization trial were visually inspected for quality in order to remove trials with obvious measurement or task errors, such as failure to reach the target, understand task instructions, or localization responses that did not land near the visually presented arc as required. For the first session which had reach training trials with an aligned cursor, 489 (1.10%) reach trials were removed and for those trials in the second session, with a cursor-rotation, 41167 older instructed (1.76%) reach trials were removed. For the first session of no-cursor reaches, 84 (3.2%) of no-cursor reaches were removed and 154 (2.9%) of no-cursor reaches in the second session were removed. For the localization responses, 209 (1.8%) of hand position estimates in the first session and 93 (0.8%) of the second session were removed. For the most, the (low) frequency of outliers was similar across the two age groups. Moreover, there was no evidence that age-related differences of our results were driven by a subset of impaired individuals; the distributions of the results were largely unimodal.

All analyses were done using R 3.4.4 (R Core Team, 2018). All statistical tests described in the Results Section used an alpha level of 0.05, and for tests where sphericity was violated, the Greenhouse-Geisser corrections were used. Partial eta-squares were used to report effect size for significant effects. Significant interactions were followed up with Welch Two Sample t-test (correcting for unequal variances and unequal sample sizes).

Results

Reach training analysis and results

To test the effect of instruction (Instructed or Non-Instructed) on initial reach adaptation between older and younger adults, the reach deviations during the first initial set of three trials, second set of three trials and the final set of 15 trials during rotated-cursor training were compared in the Instructed and Non-instructed conditions and for the two Age groups (Figure 5). A 2 x 2 x 3 mixed ANOVA with Age (Younger and Older) and Instruction (Instructed or Non-instructed) as between-subject variables and Trial Sets (First, Second and Final sets of trials) as a within-subject variable was conducted. As shown in Figure 5, all participants, regardless of Instruction and Age, Reach Deviations significantly increased across Trial Sets (Figure 7B), F (2, 150) = 94.81, $p < 0.001$, $\eta^2 = 0.48$, as required to compensate for the cursor rotation. This compensation across Trial Sets varied with Instruction, F (2, 152) = 10.45, $p < 0.0001$, $\eta^2 = 0.082$ (Interaction Trial-set X Instruction). More importantly, the interaction between Age and Instruction on Reach Deviation was significant, F (1, 75) = 4.63, p <0.035, η^2 =0.022. Showing that the ability to use instructions or not across trial sets to compensate for the perturbation does depend on whether the participant was older or younger.

However, prior research showed that instruction, or explicit strategies, mainly affected adaptation during early training (Taylor & Ivy, 2014; Werner, Benson, Anguera, & Seidler, 2011). Therefore, we compared Age (Older and Younger) and Instruction type (Instructed and Non-Instructed) for the initial two sets of trials separately in two follow-up ANOVAs.

For the First Trial Set, a 2 x 2 ANOVA with Instruction (Instructed and Non-Instructed) and Age (Older and Younger) on Reach Deviations shows that the main effect of Instruction was significant, F (1, 75) = 32.32, p < 0.0001, η^2 =0.301, and the interaction between Age and Instruction was significant, F (1, 76) = 4.72, p < 0.033, η^2 =0.059. A planned follow-up t-test on the effect of Instruction on Reach Deviation for the First Trial Set between Age groups (Older and Younger) was significant, t (33.34) = 2.71, p < 0.05, η^2= 0.06. That is instructed older adults had one-third smaller Reach Deviations (violet line in Figure 5A & 5B) than instructed younger adults (orange line). Nonetheless, another t-test on Instructed and Non-instructed older adults shows that instructed older adults (Figure 5A &B: Solid blue) produced greater Reach Deviations than Non-instructed older adults (Figure 5A &B: dashed-purple line), t (36) = -2.06, p < 0.047, η^2 =0.106. In summary, for the First Set of Trials, Reach Deviations were larger (greater cursor compensation) for the Instructed groups compared to the Non-Instructed ones, but these were not as large for the instructed older adults compared to the instructed younger adults.

The age-related difference in Reach Deviations as a function of Instruction on learning was tested for the Second Set of Trials using a 2 x 2 ANOVA with Age (Older and Younger) and Instruction (Instructed or Non-Instructed) as between subject factors. Instruction still led to overall greater Reach Deviations for the Second Trial Set, which suggests instructions still provided a benefit in this next set of trials, F (1, 75) = 4.98, $p < 0.05$, η^2= 0.077. However, this benefit of instructions did not vary with age (Interaction: Age X Instruction), F (1, 75) = 1.98, p = 0.17, η^2= 0.03. And as illustrated in Figure 5, by the last trial set, all groups attain near perfect compensation (reach deviations of roughly 30°).

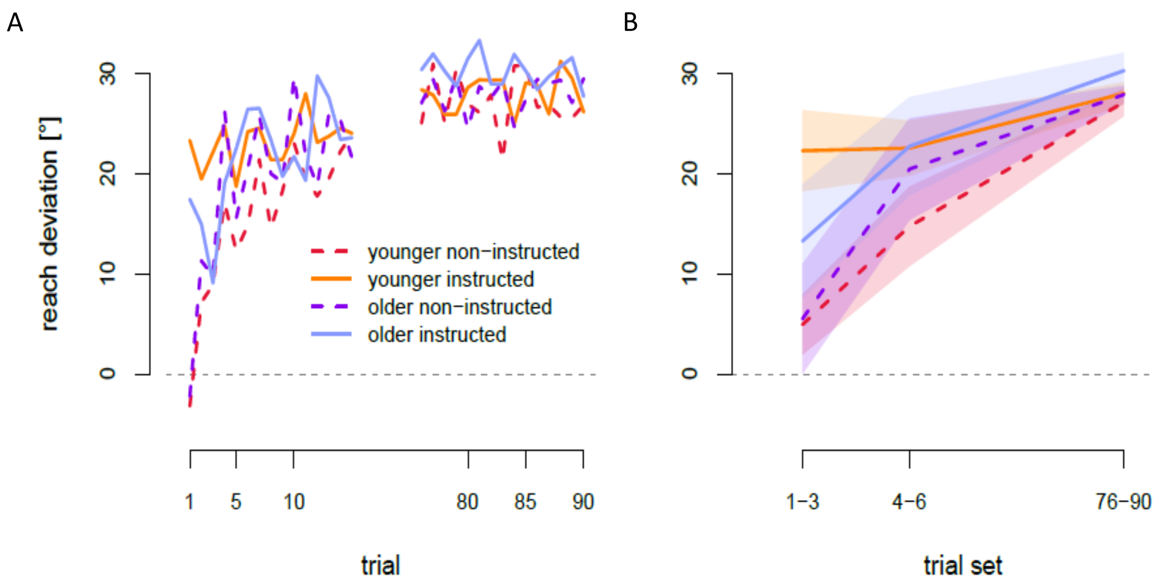


Figure 5: Changes in Reach deviations across the first 90 training trials with rotated cursor (A) and Initial, Second and Final Trial Sets (B) as function of Instruction and Age, when adapting to a 30° cursor rotation. Shaded areas represent 95% confidence intervals.

No-cursor reaches analysis and results

No cursor reaches are used to assess cognitive awareness of the cursor rotation developed during training with a rotated cursor both as a function of Age and of Instruction. For those aware of the cursor rotation, their no-cursor Reach Deviations when asked to reach with a strategy should be larger than those when asked not to use the strategy. For those who are not aware, there should be no difference between these two no-cursor reach tasks. This is the third independent variable: Strategy-Use (With and Without Strategy). However, first it was necessary to verify that No-Cursor Reach Directions did change with Training (Session 1: Aligned visual feedback and Session 2: Rotated visual feedback); that is, that these reach aftereffects were significant by comparing No-Cursor Reach Directions (for the Without Strategy trials) following rotated cursor training with No-Cursor Reach Directions produced during baseline using a three-factor ANOVA that included Training Session (Session 1: Aligned visual feedback and Session 2: Rotated visual feedback), and Instruction (Instructed and Non-instructed) and Age (Older and

Younger) as between-subject variables. As expected, significant reach aftereffects of approximately 15° CCW (larger no-cursor Reach Deviations for the Second Session than the first Session) did emerge in the Without Strategy No-Cursor Reaches, $F(1, 75) = 746.93$, $p < 0.0001$, $\eta^2 = 0.75$.

Since the main effect of Training (Session 1: Aligned visual feedback and Session 2: Rotated visual feedback) is confirmed; only the difference in no-cursor reaches relative to baseline, i.e. No-cursor Reach Deviations, as a function of the remaining two factors (Age and Instruction) and Strategy Use (within-factor) are analyzed using a 2 x 2 x 2 ANOVA. The Strategy Use manipulation allowed us to measure whether awareness of this cursor-rotation varied with Age, using a more objective measure following training with a visuomotor rotation known as the process dissociation procedure (PDP). As shown in Figure 6, older adults have, on average, roughly 20% larger no-cursor reach deviations than younger adults, $F(1, 75) = 5.66$, $p = 0.02$, $\eta^2 = 0.07$. Although everyone had adapted fully (e.g. Reach Deviations nearly 30°) for the cursor rotation during training prior to these no-cursor reaches, only those given Instruction produced the larger no-cursor Reach Deviations when asked to use the strategy (right side of Figure 6) when compared to not using the strategy (left side of Figure 6), $F(1, 73) = 31.78$, $p < 0.0001$, $\eta^2 = 0.12$ (Strategy Use X Instruction interaction). More importantly, older adults (blue and purple) show the same PDP pattern (With and Without strategy) as younger adults (orange and red), in that there is no significant interaction between Age and Instruction on No-cursor Reach Deviations, $F(1, 73) = 1.46$, $p = 0.23$, $\eta^2= 0.006$, . In other words, instructed older adults (blue) do not perform the strategy no-cursor reach any differently than instructed younger adults (orange). This suggests that despite smaller Reach Deviations for instructed older adults during the First Trial Set, instructed older adults are able to evoke the strategy during these no-cursor reaches when asked, and they do so to the same extent as younger instructed adults.

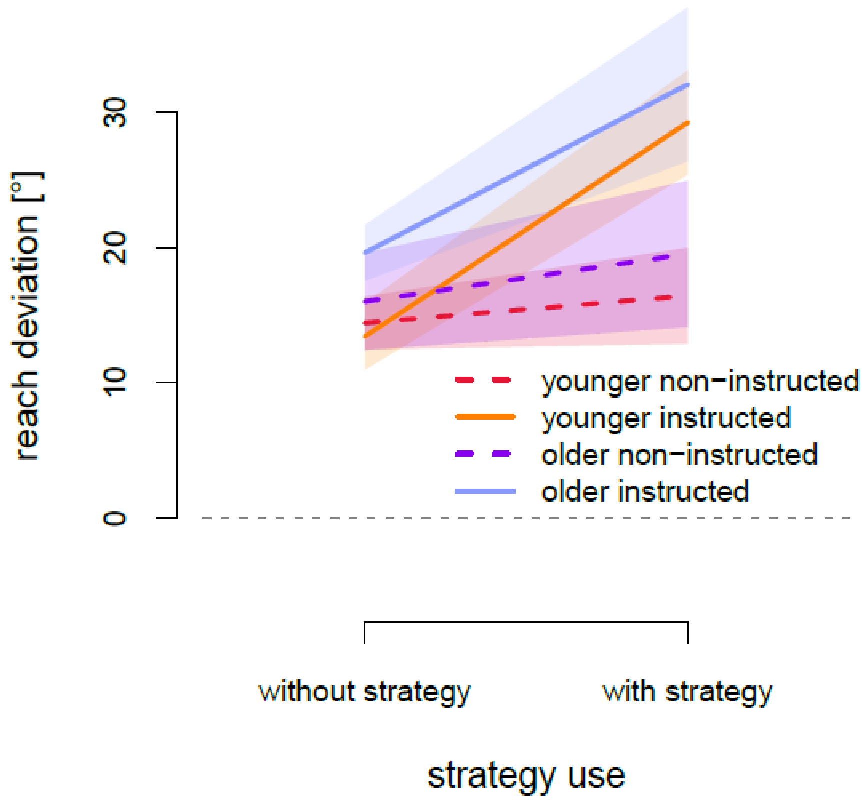


Figure 6. Strategy use: No-cursor reaches With Strategy no-cursor reaches (right side) and Without Strategy no-cursor reaches (left side). Shaded areas represent 95% confidence intervals.

Hand localization analysis and results

Next, the effect of Age and Instruction on Proprioceptive Hand Shifts as well as Updated Predicted Hand Shifts (Figure 7) is evaluated. First, we confirmed that training with a rotated cursor induces larger shifts in Hand-Position Estimates for the trained, right hand before and after training with a rotated cursor using a four-way 2X2X2X2 mixed- ANOVA that included Training Session (First session and Second Session) and Movement Type (Active and Passive localization) as within-subject factors, and Age (Older and Younger) and Instruction type (Instructed and Non-instructed) as between-subjects factors. Overall, larger shifts in Hand Localization happened in the second session compare to the first one, $F(1, 75) = 231.34$, $p<.001$, $\eta^2 = 0.28$. Moreover, Training Session significantly interacted with Movement Type, $F(1, 75) = 10.01$, $p<.002$, $\eta^2 = 0.002$. Thus, the results replicate prior findings ('t Hart & Henriques, 2016) of a significant effect of Movement Type; that is, Shifts in Hand Position Estimates in the Active version is larger from Proprioceptive Hand Shifts in the Passive version of localization tasks.

Given that the rotated-cursor training lead to a significant Shift in Hand Position Estimates, and that these Shifts vary with Movement Type (Training * Movement Type), the next step was to test whether Age and Instruction affected Proprioceptive and Updated Predicted Hand Shifts. The different localization shifts were analyzed separately for each task using two 2 x 2 ANOVAs on shifts in Hand Estimates with Age and Instruction Type as between-subjects factors. Again, the Passive Localization Shifts in Hand Estimates is referred to as Proprioceptive Hand Shifts to indicate that these shifts reflect mostly recalibrated proprioception (Figure 7B). Updated Predicted Hand Shifts (Figure 7C) were calculated by subtracting the Shifts in Hand Position Estimates during the Passive localization task (Figure 7B) from those during Active localization task (Figure 7A). In the Passive localization task, older adults (purple lines) produced significantly larger Shifts in Proprioceptive Hand Shifts, almost double that of younger adults (orange lines), F (1, 75) = 7.07, p < 0.001, η^2 = 0.067, and this did not vary with Instruction (Instructed and Non-instructed: indicated by different line styles), F (1, 75) = 0.90, p =0.35, η^2= 0.009, suggesting that Instruction does not affect these Shifts. Lastly, there is no interaction between Instruction and Age, F (1, 75) = 0.02, p =0.88, η^2 <0.001.

Although the interaction between Training (Session 1: Aligned visual feedback and Session 2: Rotated visual feedback) and Movement Type (Active and Passive Localization) on Hand Estimates was significant, a comparison between Figure 7A and 7B, and their difference in Figure 7C, and the small effect size, shows that the increased Shifts in Active Localization (i.e., the Updated Predicted Hand Shifts) are very small overall. This suggests that the shift in localization seen during the Active version (Figure 7A) can be attributed almost entirely to proprioceptive recalibration (Figure 7B). Further, the interaction between Movement-Type and Age (Movement Type X Age interaction) from the original 2x2x2x2 ANOVA is not significant, F (1, 75) = 1.59, p = 0.21, η^2< 0.01. Thus, the small changes in Updated Predicted Hand shifts do not seem to vary between older and younger adults.

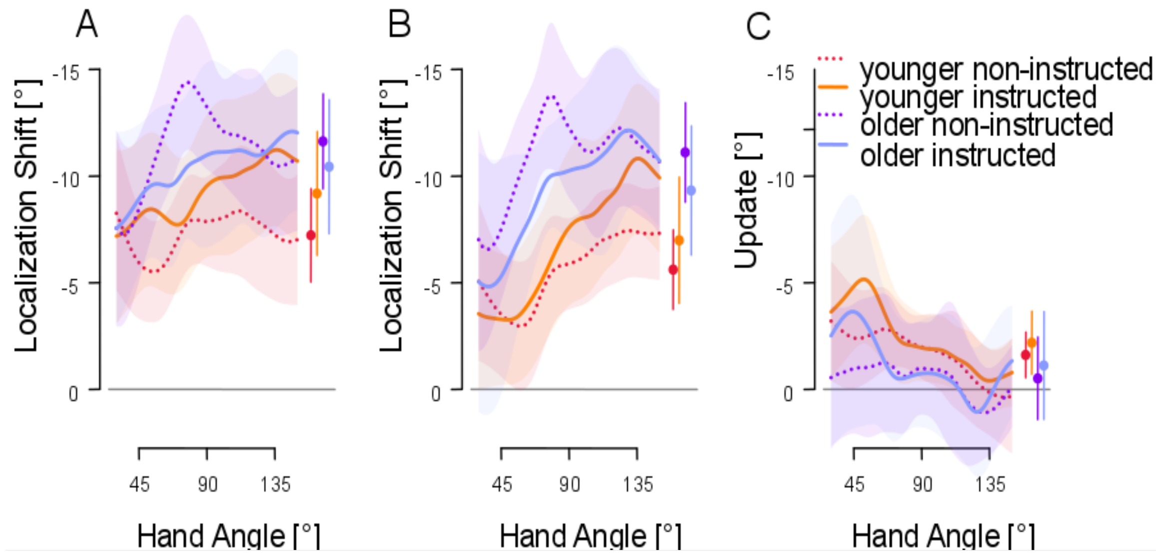


Figure 7. Changes in localization of the unseen hand following visuomotor adaptation. A. Active localization: Mean shift in hand localization estimates after training where participants actively moved their unseen right hand to a location of their choosing on the white arc (Efferent and afferent). B. Passive Localization: Mean shift in hand localization estimates after training where the unseen right hand is passively moved to the exact location as the active localization task (Only afferent). C: Predicted sensory consequences: Differences in estimates between active hand localization (efferent and afferent) and passive hand localization (afferent only). This difference should isolate changes in efferent-based estimates of hand location. Shaded areas are 95% confidence intervals.

Since previous results by ’t Hart and Henriques (2016) suggested that changes in Active localization should at least partly reflect updated prediction (that active localization should be larger than passive), the differences in Active and Passive localization are compared using a 2X2 ANOVA on Updated Predicted Hand Shifts with Age and Instruction as factors. Again, there is no difference on Updated Predicted Hand Shifts as a function of Age, $F(1, 75)=1.59$, $p=0.19$, $\eta^2= 0.02$. However, comparing the magnitude of these Updated Predicted Hand Shifts for each age group shows that the 0.84° shift for older adults did not significantly differ from 0, t (35) = 1.07, p = 0.15, whereas, Updated Predicted Hand Shifts of 1.97° in the younger adults did significantly differ from 0, $t(41)=4.62$, $p<.001$. These results are consistent with the confidence intervals illustrated in Figure 9C. In summary, while older adults show much greater proprioceptive recalibration (larger Proprioceptive Hand Shifts) than younger adults, they do not show detected changes in Updated Predicted Hand Shifts. Nonetheless, this is not significantly different from the small changes that are detected in younger adults.

Discussion

In this study, the effects of age-related changes in cognitive capabilities on strategy use in learning, and the effects of age-related changes in sensory acuity on shifts in hand localization were assessed. The first aim was to test the extent older adults are capable of using a cognitive strategy to initially adapt to a visuomotor rotation. We showed that older adults are initially less able to make use of instructions to adapt hand movements compared with their instructed younger counterparts. This is not due to instructed older adults' inability to understand the strategy because they demonstrated that they were able to include or exclude their strategy when reaching without cursor. The second aim assessed how location estimates of the unseen, trained hand changed after training with a visuomotor rotation as a function of age. We found that proprioceptive recalibration is greater in older than younger adults, but providing instructions that clarified the nature of the perturbed feedback did not change how the altered feedback influenced the estimates of hand location. In addition, we found that older adults showed no updates in their efference-based predictions of sensory consequences of their movements after training. In short, the benefit of instruction at the very start of visuomotor adaptation was slightly smaller in older adults. In addition, older adults recalibrated their proprioceptive estimates of hand location to a much larger extent than younger adults, but showed no noticeable difference in their updated predicted sensory consequences.

Instruction facilitates initial adaptation

Our findings replicated prior research that demonstrated that instruction on how to counteract a perturbation can benefit initial adaptation (Benson et al., 2011; Hegele & Heuer, 2013; Taylor, Krakauer, & Ivry, 2014; Werner et al., 2015). Werner et al., (2015) and Benson, Anguera, and Seidler (2011) gave the same instruction to younger adults as in our study on how to adapt to a visuomotor rotation. These instructed younger participants showed the same benefit as in our study: they compensated for the rotated feedback at the start of training. Taylor et al. (2014) showed a smaller benefit (increase in learning rate) of instruction to their younger adults, and interpreted this small effect as an early explicit contribution occurring in both instructed and non-instructed groups (as illustrated by their aiming strategy in the instructed group) when adapting to a visuomotor rotation. This early explicit contribution is followed by and largely taken over by implicit processes. The effect of instruction on initial adaptation has been shown to be related to cognitive processes such as spatial working memory (Anguera et al., 2012, 2010, 2011; Christou, Miall, McNab, & Galea, 2016; Seidler & Carson, 2017; Seidler, Mulavara, Bloomberg, & Peters, 2015) and this ability appears to be somewhat decreased in older as compared to younger adults (Anguera et al., 2011; Seidler, 2006).

The use of instruction in our study [based on that of Benson, Anguera, & Seidler, (2011) and Werner et al. (2015)] did help all age groups, but the effect on initial learning for older adults was 33% smaller than for younger adults. Other studies have also found that older adults benefit less from instruction. For example, Heuer and Hegele (2008a &b; 2013) demonstrated that, when both given instruction and corrective feedback, older adults were less able to acquire or apply a cognitive strategy when training to rotate an arrow toward the direction they would have to move to compensates for the 75° visuomotor rotation. However, it is unclear when differences in the acquisition and application of an adaptive strategy emerged in learning as they averaged out performance across trials. Here, the age-related differences in applying a cognitive strategy for a smaller rotation of 30° were limited to the initial stages of learning and not at the end of learning. This suggests that the ability or willingness to adopt a novel explicit strategy decreases with age. Other age-related deficits can emerge even in the absence of instruction (Lei & Wang, 2017; Seidler, 2006). However, this study showed no differences in the non-instructed older adults compared to the younger non-instructed adults. The difference between the current results and those showing an aging-deficit in visuomotor adaptation could be attributed to the size of the rotation and its implication on cognitive awareness of the visual perturbation (Benson et al., 2011; Cressman et al., 2010; Werner et al., 2015). As the size of the rotation increases (greater than 45°), there are larger initial differences in learning between older (greater than 55 years old) and younger adults (Heuer & Hegele, 2008b; Heuer et al., 2011; Simon & Bock, 2016). For smaller rotations (e.g. 30° rotation) the findings are less consistent: some studies finding older adults sometimes initially adapt less than younger adults (Anguera et al., 2010; Lei & Wang, 2017; Seidler, 2006) and others, like the current study, find no such age-related differences (Heuer & Hegele, 2008b) in the absence of instruction. Thus, it may be with larger perturbations, cognition is more likely to engage and play a larger role and any deficits in using a strategy may emerge. This study and others found no age-related differences in the non-instructed adults' initial adaptation, which suggest that reach adaptation for smaller perturbation is intact in older adults. Thus, for the most part, the small perturbations that one would experience in everyday life are likely handled quite well in healthy older adults.

In order to better test awareness or development of a cognitive strategy during training, a post-training test known as a process dissociation procedure (PDP) was given. The PDP consisted of asking participants to use or not use any strategies that they developed during a visuomotor adaptation when reaching without any visual feedback (No cursor). Those who were told how to counter the cursor-rotation or who became aware of the nature of the perturbation in another way were able to evoke the strategy when asked; thus producing larger hand deviations compared to not applying the strategy. This produced a non-verbal more objective measure of awareness of the perturbation or explicit learning. In the present study, both non-instructed and instructed groups compensated fully for the relatively small cursor rotation, yet only those who received instructions were able to evoke larger hand movement deviations when asked during no-cursor reaches following training. Others have demonstrated that larger rotations (e.g. 60°), even in the absence of instruction, can lead to PDP awareness in young adults (Werner et al., 2015) For example, using tasks that largely mimic the PDP, Heuer and Hegele (2008; 2013) found that adapting to a 75° visuomotor rotation led to much larger no-cursor hand deviations when told to reach as if there was a rotated cursor compared to when told to reach without a rotation (i.e. reach aftereffects), but only in younger adults. Older adults showed no differences in reach deviation when cued to reach as if the cursor rotation was there or not in these no-cursor reaches. Across age groups, the pattern of deviations of reaches made with an “invisible” cursor when asked to reach with or without a rotation, was similar to the pattern seen in another measure of Heuer and Hegele (2008; 2013) that involved aiming a white line to the intended reach direction (discussed further below). The PDP demonstrated that, despite the initial task performance differences between instructed older and younger adults, older adults were able to include the strategy to the same extent as younger adults when asked to do so while reaching without a cursor. This suggests that the initial cognition-related learning differences were due to an inability to and preference not to immediately deploy the strategy, but not to an inability to understand the instruction or the ability to develop a strategy, at least when the rotation was small.

Spatial working memory and motor learning

Research has increasingly shown that initial learning is closely related with a cognitive sub-component of attention: spatial working memory (SWM). Exploring the relationship between cognition and motor learning, Christo et al. (2016) showed that a small portion of younger participants with poor SWM also showed a smaller explicit contribution in their learning. Likewise, Anguera, Reuter-Lorenz, Willingham, and Seidler (2010) found that some SWM tasks do predict initial adaptation rate to a 30° visuomotor adaptation in younger adults, but not older adults. They also found that older adults adapted more slowly than younger adults in response to a visuomotor rotation. Moreover, while younger adults show overlapping neural activities during the early adaptation period and the SWM performance, other adults do not show the same overlap. Given the possible importance of SWM in initial visuomotor learning, Anguera et al. (2010) suggested that the lack of activation of SWM-related brain areas in older adults during visuomotor adaptation, despite normal brain activity in other tasks, may be related to their failure to effectively engage SWM processes during learning. This in turn could explain age-related deficits in visuomotor adaptation. Although, we did not directly test differences in SWM across groups and found no age-related differences in early adaptation rate for our non-instructed groups, it cannot be ruled out that age-related changes in cognition, which should include SWM, may have led older participants to benefit less from instructions when initially adapting to the visuomotor rotation.

Proprioceptive recalibration and aging

Instructions contribute to motor learning across the age spectrum, but so does the quality of the sensory feedback in our limbs. The current findings support that training with altered visual feedback of the hand shifts the perceived hand position towards the prior visual experience, known as proprioceptive recalibration (Cameron et al., 2012; Clayton et al., 2014; Cressman & Henriques, 2009; Cressman et al., 2010; Henriques et al., 2014; Mostafa et al., 2015; Ruttle, 't Hart, & Henriques, 2018; Ruttle et al., 2016). This recalibration is approximately 20% of the size of visual distortion and it occurs only for the trained hand (Cameron et al., 2012; Mostafa Salomonczyk, Cressman, & Henriques, 2014). It emerges very quickly (Ruttle et al., 2016) and arises for different rotation sizes (Salomonczyk, Cressman, & Henriques, 2013), and under different types of feedback such as visual feedback only at the end of the reach compared to continuous cursor feedback (Barkley et al., 2014). In short, proprioceptive recalibration is a common and robust process that seems to accompany visuomotor adaptation.

Unsurprisingly, we replicated the finding that proprioceptive recalibration occurs independent of age (Cressman et al., 2010). Many studies show that as age increases, the quality of sensory feedback diminishes (Cressman et al., 2010; Goble et al., 2009; Lei & Wang, 2017; Wolpe et al., 2016). However, it is unclear how the decrease in the acuity of proprioceptive feedback affects proprioceptive recalibration. Cressman et al. (2010) demonstrated older and younger adults shift the position of their felt hand to coincide with a reference marker after training with a cursor gradually rotated 30° using a two-alternative forced choice method. All age groups recalibrated their proprioception roughly 6°, i.e., approximately 20% of the visuomotor distortion introduced; however, our findings show a larger recalibration with age. Using our passive localization task, we found that older adults produced twice as large of a shift in hand estimations as compared to younger adults. A difference between our study and that of Cressman et al. (2010) is in the method used to measure proprioceptive change. Our passive localization task involved was having the visible, left hand indicate the remembered location of the unseen right hand on a visible arc. This method has been shown to produce similarly sized changes in proprioception (Clayton et al., 2012) in younger adults. Plus, it appears that this faster method of measuring proprioceptive change is less vulnerable to decay [compare Ruttle et al., (2016) with Zbib, Henriques, & Cressman (2016)]. Thus, it may be that age-related differences were more detectable in the localization task than in Cressman et al. 2010. Additionally, it may be differences in the same size of the two studies. The participants in Cressman et al., 2010 were a few years younger (average of 66 years old) compared to those in the current study (70 years old) and they had a far small number (9 vs 38). Thus, the current sample size was four times larger than Cressman et al. (2010) potentially providing more power to detect a difference in a slightly older population.

Altogether, our findings suggest that proprioceptive recalibration is greater in older adults. The larger proprioceptive hand shifts or recalibration in older adults may be due to greater reliance on visual over proprioceptive feedback. This could be because older adults' sensory acuity is poorer than younger adults (see Goble et al., 2009 for a review). For example, recently Lei and Wang (2017) demonstrated that older adults were less precise in actively matching their right arm to their unseen left arm's passively moved position even prior to any training. Cressman et al. (2010) also showed that older adults had a 25% larger uncertainty range in estimating the unseen hand compared to younger adults. Together, there appears to be a persistent pattern that suggests a relationship between increasing age and diminishing sensory acuity (Goble et al., 2009; Lei & Wang, 2017; Wolpe et al., 2016). While our results are compatible with an age-related decline in proprioceptive acuity, it is still unclear if predictive hand estimates change with age.

Updated Prediction with Age

Motor learning does not only lead to changes in proprioceptive estimates of hand position, but updates predicted estimates as well. ’t Hart and Henriques (2016) found that learning induced changes in hand localization reflected mostly a change in proprioception (about 66%) compared to prediction (the remaining 33%). In our study (which included more targets and trials), this proportion was even more skewed, with younger adults showing a change in hand localization that reflected 80% change in proprioception and 20% change in prediction. The change in predictive estimate of hand position was further reduced in older adults, such that the 1 to 2° change was not statistically detectable (although their proprioceptive change was 50% larger than that of younger adults). This difference was not significant relative to younger adults since the changes for younger adults were also quite small; approximately 20% of the changes reflecting only 2 to 3° of the shift (Figure 8C). There are several possible reasons for this. First, the absence in changes in Updated Predicted Hand Shifts for older adults might be due to their larger change in Proprioceptive Hand Shifts. Such a large change in proprioception may act as a ceiling effect or generally mask any further change due to prediction. Alternatively, it could be that older adults are more reliant on previous predicted estimates, which are based on a “longer” lifetime of daily movements, that they may be more resistant to changes or updating these predicted estimates even in the face of the perturbation. In fact, other studies suggest that as long as the cerebellum is intact, older adults may even rely more on prediction. For example, in a very different study that required matching felt force on the finger, Wolpe and colleagues (2016) suggested that older adults may rely more on predictions from prior sensory experience in life in light of degrading sensory feedback. Similarly, age-related increases in sensory noise may lead to greater reliance on efference signals (or predicted sensory consequences) to compensate for changes in motor control. Thus, it is possible that when localizing the hand or body, older adults may rely more on the predicted sensory consequences of a movement due to age-related noisy proprioceptive feedback. This age-related inflation of proprioceptive recalibration but absence of age-related predictive changes could suggest that age does not produce deficits in using and updating forward computations (efference-based or predicted sensory consequences).

Studies have attempted to investigate changes in the efferent-based or predicted estimate of hand position following visuomotor learning by measuring learning-induced changes in estimates of the unseen hand after the movement has been self-generated (Izawa et al., 2012; Synofzik et al., 2008). Using the equivalent to active localization, Synofzik et al. (2008) and Izawa et al. (2012) examined how the estimates of hand location change when the hand movement is self-generated in healthy adults and patients with cerebellum damage after adapting to a visuomotor rotation. Both groups found that learning-induced changes in estimates of the location of the unseen hand in both healthy participants and cerebellum patients, but the shift in hand localization estimates were only half the size in the patient group. Based on this, both studies concluded that the cerebellum is critical for updating the predicted consequences of movements during learning. However, the remaining shifts in the patient group may not only be due to changes in prediction, given that proprioception also changes following visuomotor learning and these changes appear to occur even in cerebellar patients (Henriques et al., 2014) as verified by ’t Hart and Henriques (2016) in healthy adults and in the current study. It is unclear how changes in the cerebellum due to age may affect changes in the predicted sensory consequences of hand movements after training with a visuomotor rotation.

Limitations

Our study had many limitations that may have affected the results. It could be that a lack of age-related differences may be due to poor power since a power analysis was not completed beforehand. However, given our large group sizes, it is unlikely that more participants would have revealed age-differences where we found none. It is possible our two age groups differed in other ways that influenced their performance in these tasks, like their level of motivation, education, health related factors, experience with technology, and cognitive abilities. None of these factors were assessed and controlled for in this study. However, the results within each group were largely unimodal, which suggests that any presence or absence of age-related findings were likely not driven by a one or two individuals who differed from the rest of the groups on any of these factors. In addition, it was also ensured that all groups understood the tasks and for the instructed groups, the cognitive strategy we gave them. Altogether, despite these limitations, the findings in this study do not contradict the majority of the literature on the acquisition and application of a cognitive strategy in older adults.

Conclusion

This study demonstrated that age does lead to a reduced benefit of instruction (smaller reach deviations) in early reach adaptation. This suggests that cognitive changes with age can contribute to the acquisition and application of a strategy to initially adapt. We also show that proprioceptive hand shifts (proprioceptive recalibration) in older adults are greater than in younger adults after training with a visuomotor rotation, independent of their awareness of this rotation. This greater proprioceptive recalibration with older age may be due to greater reliance on vision over proprioception; perhaps due to declines in proprioceptive acuity. However, it appears that aging does not affect the updating of predicted hand shifts after training with altered visual feedback. This study shows that aging may lead to subtle, yet important changes, in sensorimotor learning and multisensory integration.

References

Anguera, J. A., Bernard, J. A., Jaeggi, S. M., Buschkuehl, M., Benson, B. L., Jennett, S., Seidler, R. D. (2012). The effects of working memory resource depletion and training on sensorimotor adaptation. *Behavioural Brain Research*, *228*(1), 107–115. https://doi.org/10.1016/j.bbr.2011.11.040

Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2010). Contributions of Spatial Working Memory to Visuomotor Learning. *Journal of Cognitive Neuroscience*, *22*(9), 1917–1930. https://doi.org/10.1162/jocn.2009.21351

Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2011). Failure to Engage Spatial Working Memory Contributes to Age-related Declines in Visuomotor Learning. *Journal of Cognitive Neuroscience*, *23*(1), 11–25. https://doi.org/10.1162/jocn.2010.21451

Barkley, V., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. P. (2014). Reach adaptation and proprioceptive recalibration following terminal visual feedback of the hand. *Frontiers in Human Neuroscience*, *8*, 705. https://doi.org/10.3389/fnhum.2014.00705

Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology*, *105*(6), 2843–2851. https://doi.org/10.1152/jn.00002.2011

Bock, O., & Girgenrath, M. (2006). Relationship between sensorimotor adaptation and cognitive functions in younger and older subjects. *Experimental Brain Research*, *169*(3), 400–406. https://doi.org/10.1007/s00221-005-0153-4

Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology*, *113*(10), 3836–3849. https://doi.org/10.1152/jn.00009.2015

Buch, E. R.; Young, S.; Contreras-Vidal, J. L. (2003). Visuomotor Adaptation in Normal Aging. *Learning & Memory*, *10*(1), 55–63. https://doi.org/10.1101/lm.50303

Cameron, B. D., Franks, I. M., Inglis, J. T., & Chua, R. (2012). The adaptability of self-action perception and movement control when the limb is passively versus actively moved. *Consciousness and Cognition*, *21*(1), 4–17. https://doi.org/10.1016/J.CONCOG.2010.11.006

Christou, A. I., Miall, R. C., McNab, F., & Galea, J. M. (2016). Individual differences in explicit and implicit visuomotor learning and working memory capacity. *Scientific Reports*, *6*(October), 1–13. https://doi.org/10.1038/srep36633

Clayton, H. A., Cressman, E. K., & Henriques, D. Y. P. (2014). The effect of visuomotor adaptation on proprioceptive localization: The contributions of perceptual and motor changes. *Experimental Brain Research*, *232*(7), 2073–2086. https://doi.org/10.1007/s00221-014-3896-y

Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1995). Oculocentric spatial representation in parietal cortex. *Cerebral Cortex*, *5*(5), 470–481. https://doi.org/10.1093/cercor/5.5.470

Craik, F. I. M., & Grady, C. L. (2009). Aging, Memory, and Frontal Lobe Functioning. In *Principles of Frontal Lobe Function* (pp. 528–540). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195134971.003.0031

Cressman, E. K., & Henriques, D. Y. P. (2009). Sensory Recalibration of Hand Position Following Visuomotor Adaptation. *Journal of Neurophysiology*, *102*(6), 3505–3518. https://doi.org/10.1152/jn.00514.2009

Cressman, E. K., & Henriques, D. Y. P. (2010). Reach Adaptation and Proprioceptive Recalibration Following Exposure to Misaligned Sensory Input. *Journal of Neurophysiology*, *103*(4), 1888–1895. https://doi.org/10.1152/jn.01002.2009

Cressman, E. K., Salomonczyk, D., & Henriques, D. Y. P. (2010). Visuomotor adaptation and proprioceptive recalibration in older adults. *Experimental Brain Research*, *205*(4), 533–544. https://doi.org/10.1007/s00221-010-2392-2

Cunningham, H. A. (1989). Aiming Error Under Transformed Spatial Mappings Suggests a Structure for Visual-Motor Maps. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(3), 493–506. https://doi.org/10.1037/0096-1523.15.3.493

Ebner, T. J., & Pasalar, S. (2008). Cerebellum predicts the future motor state. *Cerebellum*, *7*(4), 583–588. https://doi.org/10.1007/s12311-008-0059-3

Fernández-Ruiz, J., Hall, C., Vergara, P., & Díaz, R. (2000). Prism adaptation in normal aging: Slower adaptation rate and larger aftereffect. *Cognitive Brain Research*, *9*(3), 223–226. https://doi.org/10.1016/S0926-6410(99)00057-9

Goble, D. J., Coxon, J. P., Van Impe, A., Geurts, M., Van Hecke, W., Sunaert, S., Swinnen, S. P. (2012). The neural basis of central proprioceptive processing in older versus younger adults: An important sensory role for right putamen. *Human Brain Mapping*, *33*(4), 895–908. https://doi.org/10.1002/hbm.21257

Goble, D. J., Coxon, J. P., Wenderoth, N., Van Impe, A., & Swinnen, S. P. (2009, March 1). Proprioceptive sensibility in the elderly: Degeneration, functional consequences and plastic-adaptive processes. *Neuroscience and Biobehavioral Reviews*. Pergamon. https://doi.org/10.1016/j.neubiorev.2008.08.012

Hegele, M., & Heuer, H. (2010). Adaptation to a direction-dependent visuomotor gain in the young and elderly. *Psychological Research Psychologische Forschung*, *74*(1), 21–34. https://doi.org/10.1007/s00426-008-0221-z

Hegele, M., & Heuer, H. (2013). Age-Related variations of visuomotor adaptation result from both the acquisition and the application of explicit knowledge. *Psychology and Aging*, *28*(2), 333–339. https://doi.org/10.1037/a0031914

Henriques, D. Y. P., Filippopulos, F., Straube, A., & Eggert, T. (2014). The cerebellum is not necessary for visually driven recalibration of hand proprioception. *Neuropsychologia*, *64*, 195–204. https://doi.org/10.1016/j.neuropsychologia.2014.09.029

Heuer, H., & Hegele, M. (2008). Adaptation to Visuomotor Rotations in Younger and Older Adults. *Psychology and Aging*, *23*(1), 190–202. https://doi.org/10.1037/0882-7974.23.1.190

Heuer, H., Hegele, M., & Sülzenbrück, S. (2011). Implicit and explicit adjustments to extrinsic visuo-motor transformations and their age-related changes. *Human Movement Science*, *30*(5), 916–930. https://doi.org/10.1016/j.humov.2010.07.004

Izawa, J., Criscimagna-Hemminger, S. E., & Shadmehr, R. (2012). Cerebellar contributions to reach adaptation and learning sensory consequences of action. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(12), 4230–4239. https://doi.org/10.1523/JNEUROSCI.6353-11.2012

King, B. R., Fogel, S. M., Albouy, G., & Doyon, J. (2013). Neural correlates of the age-related changes in motor sequence learning and motor adaptation in older adults. *Front Hum Neurosci*, *7*(April), 142. https://doi.org/10.3389/fnhum.2013.00142

Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *20*(23), 8916–8924. https://doi.org/20/23/8916 [pii]

Lei, Y., & Wang, J. (2017). The effect of proprioceptive acuity variability on motor adaptation in older adults. *Experimental Brain Research*, *0*(0), 1–10. https://doi.org/10.1007/s00221-017-5150-x

’t Hart, B., & Henriques, D. Y. P. (2016). Separating Predicted and Perceived Sensory Consequences of Motor Learning. *PLOS ONE*, *11*(9). https://doi.org/10.1371/journal.pone.0163556

Mazzoni, P. . K. J. W. (2006). An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *Journal of Neuroscience*, *26*(14), 3642–3645. https://doi.org/10.1523/JNEUROSCI.5317-05.2006

Moran, R. J., Symmonds, M., Dolan, R. J., & Friston, K. J. (2014). The Brain Ages Optimally to Model Its Environment: Evidence from Sensory Learning over the Adult Lifespan. *PLoS Computational Biology*, *10*(1), e1003422. https://doi.org/10.1371/journal.pcbi.1003422

Mostafa, A. A., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. P. (2014). Intermanual transfer and proprioceptive recalibration following training with translated visual feedback of the hand. *Experimental Brain Research*, *232*(6), 1639–1651. https://doi.org/10.1007/s00221-014-3833-0

Mostafa, A. A., Kamran-disfani, R., Bahari-kashani, G., Cressman, E. K., & Henriques, D. Y. P. (2015). Generalization of reach adaptation and proprioceptive recalibration at different distances in the workspace. *Exp Brain Res*. https://doi.org/10.1007/s00221-014-4157-9

Neva, J. L., & Henriques, D. Y. P. (2013). Visuomotor adaptation and generalization with repeated and varied training. *Exp Brain Res*, *226*, 363–372. https://doi.org/10.1007/s00221-013-3444-1

Ostry, D. J., Darainy, M., Mattar, A. A. G., Wong, J., & Gribble, P. L. (2010). Somatosensory Plasticity and Motor Learning. *Journal of Neuroscience*, *30*(15), 5384–5393. https://doi.org/10.1523/JNEUROSCI.4571-09.2010

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging*, *17*(2), 299–320. https://doi.org/10.1037/0882-7974.17.2.299

Rand, M. K., Wang, L., Müsseler, J., & Heuer, H. (2013). Vision and proprioception in action monitoring by young and older adults. *Neurobiology of Aging*, *34*(7), 1864–1872. https://doi.org/10.1016/j.neurobiolaging.2013.01.021

Ruttle, J. E., ’t Hart, B. M., & Henriques, D. Y. P. (2018). The fast contribution of visual-proprioceptive discrepancy to reach aftereffects and proprioceptive recalibration. *PLOS ONE*, *13*(7), e0200621. https://doi.org/10.1371/journal.pone.0200621

Ruttle, J. E., Cressman, E. K., Marius ’t Hart, B., & Henriques, D. Y. P. (2016). Time Course of Reach Adaptation and Proprioceptive Recalibration during Visuomotor Learning. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0163695

Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. P. (2011). Proprioceptive recalibration following prolonged training and increasing distortions in visuomotor adaptation. *Neuropsychologia*, *49*, 3053–3062. https://doi.org/10.1016/j.neuropsychologia.2011.07.006

Salomonczyk, D., Henriques, D. Y. P., & Cressman, E. K. (2012). Proprioceptive recalibration in the right and left hands following abrupt visuomotor adaptation. *Experimental Brain Research*, *217*(2), 187–196. https://doi.org/10.1007/s00221-011-2985-4

Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. P. (2013). The role of the cross-sensory error signal in visuomotor adaptation. *Experimental Brain Research*, *228*(3), 313–325. https://doi.org/10.1007/s00221-013-3564-7

Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin*, *70*(4–6), 337–346. https://doi.org/10.1016/j.brainresbull.2006.06.008

Seidler, R. D., & Carson, R. G. (2017). Sensorimotor Learning: Neurocognitive Mechanisms and Individual Differences. *Journal of NeuroEngineering and Rehabilitation*, *14*(1), 74. https://doi.org/10.1186/s12984-017-0279-1

Seidler, R. D., Mulavara, A. P., Bloomberg, J. J., & Peters, B. T. (2015). Individual predictors of sensorimotor adaptability. *Frontiers in Systems Neuroscience*, *9*, 100. https://doi.org/10.3389/fnsys.2015.00100

Simon, A., & Bock, O. (2016). Influence of divergent and convergent thinking on visuomotor adaptation in young and older adults. *Human Movement Science*, *46*, 23–29. https://doi.org/10.1016/j.humov.2015.11.020

Synofzik, M., Lindner, A., & Thier, P. (2008). The Cerebellum Updates Predictions about the Visual Consequences of One's Behavior. *Current Biology*, *18*(11), 814–818. https://doi.org/10.1016/j.cub.2008.04.071

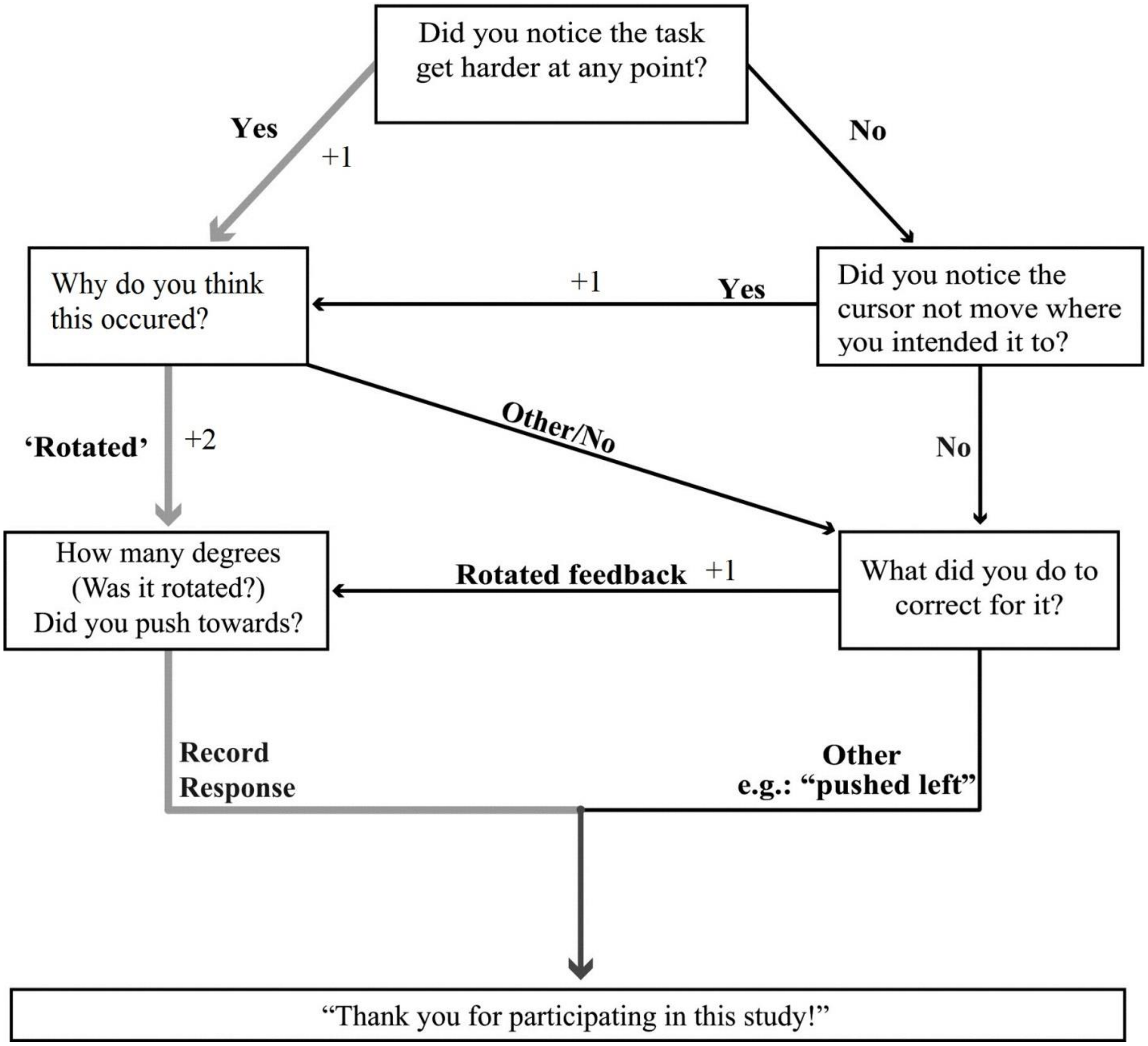
Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, *34*(8), 3023–3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Werner, S., Van Aken, B. C., Hulst, T., Frens, M. A., Van Der Geest, J. N., Strüder, H. K., & Donchin, O. (2015). Awareness of sensorimotor adaptation to visual rotations of different size. *PLoS ONE*, *10*(4), e0123321. https://doi.org/10.1371/journal.pone.0123321

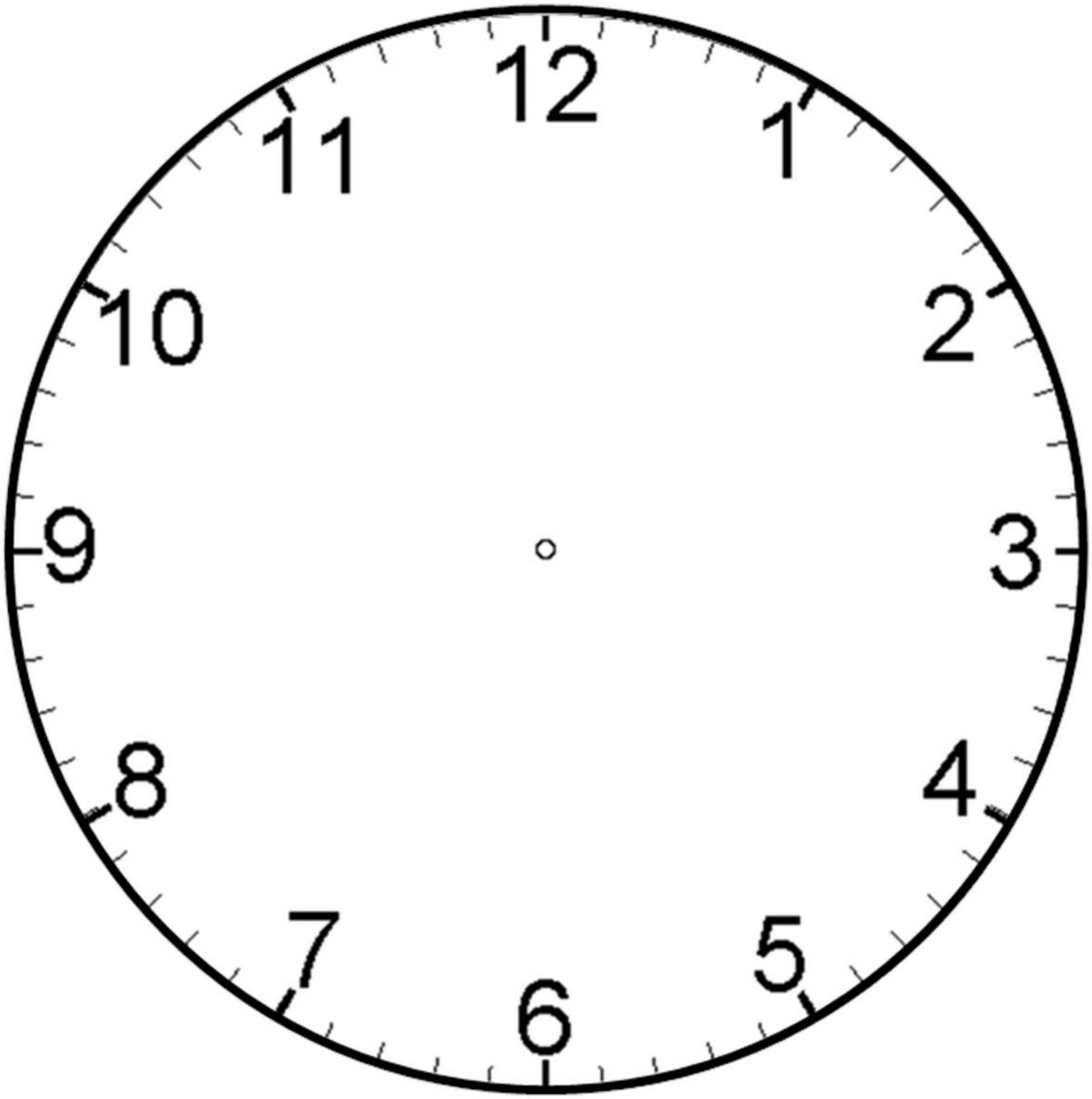
Wolpe, N., Ingram, J. N., Tsvetanov, K. A., Geerligs, L., Kievit, R. A., Henson, R. N., Rowe, J. B. (2016). Ageing increases reliance on sensorimotor prediction through structural and functional differences in frontostriatal circuits. *Nature Communications*, *7*, 1–11. https://doi.org/10.1038/ncomms13034

Appendices

Appendix A: Questionnaire for awareness at the end of the experiment.



Appendix B: Clock diagram used in explanation of the cursor rotation.



Appendix C: Verbal instructions

Intro

In this experiment you will be completing a variety of tasks while using your right hand to grip the handle of a robotic arm (place thumb on top of screw). The robot handle can be moved by you or it can mechanically guide your movements, depending on the task. At some points you will be responding to stimuli displayed on the touch screen in front you and using your left hand to touch certain spots reached by your right hand.

Cursor

The green cursor on the screen represents your hand position – specifically the thumb. You are going to be reaching to the yellow target while gripping and moving the robot handle. The cursor has to overlap with the target for the trial to be complete. After completing the reach you wait for the target to disappear and then move the handle back to the starting position. Then you can remain still and wait for the next trial to begin. Try to move your hand to the target as quickly and accurately as possible.

Active Trials

In this task you are going to see an arc. Your task is to reach with your unseen right hand (while gripping the robot handle) to intersect the arc at a point you choose. As this task repeats try to reach to intersect different sections of the arc instead of just one point. The more areas of the arc you intersect the less time this experiment will take. After intersecting the arc, you pull your arm back to the starting position. Next, you will use your left hand to indicate on the touch screen where your right hand crossed the arc. Once you have touched on the screen with your left hand, retract your hand and place it under your chin (demonstrate).

Passive trials

In this task you are going to see an arc just like before. However, the robot will move your unseen hand to a specific part of the arc. Let the robot guide your arm movement; don't resist. As before, you will indicate where your right hand crossed the arc, with your left hand and remove the left hand from the touch screen in between trials.

No Cursor

In this task you are going to reach to targets but this time there is no cursor indicating your hand position. Your task, like before, will be to reach to the target as accurately as possible. After completing the reach – when you think you have reached the target – keep your hand still. Keeping your hand still informs the robot the trial is complete, and the target will disappear. Then move the handle back to the starting position, and wait for the next trial to begin.

Explaining Perturbations/Rotation task (for explicit)

For these next few reaching tasks, the green cursor will move a bit differently. The cursor is not going to move in the same direction as your hand and you will need to compensate for this. [SHOW DEMO]. Imagine your starting point as being at the centre of a clock face, and you move your hand to the 12 position at the top. As you move your hand from the centre to the 12, the cursor will move to the right to 1 on the clock. Aim for the 11on the clock so that your cursor ultimately reaches the target at 12. Did I explain this clearly?
Keep these instructions and strategy in mind since you will be asked to use this strategy several times, including when reaching without a cursor. Sometimes you will be asked to NOT use this strategy when reaching without a cursor.

Explaining Perturbations/Rotation task (for implicit)
For these next few reaching tasks, the green cursor will move a bit differently, and you will need to compensate for this.
However you compensate, keep that strategy in mind since you will be asked to use this strategy several times, including when reaching without a cursor. Sometimes you will be asked to NOT use this strategy when reaching without a cursor.

Don't use strategy from earlier - Exclusive
For this next task you will be reaching to a target without a cursor. For THESE trials, do not make use of any strategies you learned earlier and treat this as you did the original baseline reach-to-target task.

Make use of strategy from earlier - Inclusive
For this next task you will be reaching to a target without a cursor. For THESE trials, please make use of the strategy you learned earlier to correct for odd movement of the cursor.

Appendix D

Informed Consent Form (for unpaid participants)

Date:

Study Name: Multisensory interaction in motor control and learning

Researchers: Dr. Denise Henriques, Chad Vachon, Marius 't Hart

Purpose of the Research: Our research team is interested in how people adapt movement of the arm towards visual targets or proprioceptive (felt but unseen hand) target, or estimate of the location or motion of their hand, under various circumstances and using multisensory information.

What You Will Be Asked to Do in the Research: You will be asked to reach or point toward visual targets displayed on a screen and/or point to your unseen other hand (felt target). This will take place in the Sensorimotor control lab in Calumet 304.

Risks and Discomforts: We do not foresee any risks or discomfort from your participation in the research.

Benefits of the Research and Benefits to You: None.

Voluntary Participation: Your participation in the study is completely voluntary and you may choose to stop participating at any time. Your decision not to volunteer will not influence your relationship with us or anyone else at York University either now, or in the future.

Withdrawal from the Study: You can stop participating in the study at any time, for any reason, if you so decide. If you decide to stop participating, you will still be eligible to receive the URPP or KURE credit (if applicable) for agreeing to be in the project. Your decision to stop participating, or to refuse to answer particular questions, will not affect your relationship with the researchers, York University, or any other group associated with this project. If you decide to stop participating, you will still be eligible to receive the URPP or KURE credit for agreeing to participate. In the event you withdraw from the study, all associated data collected will be immediately removed from our computers.

Confidentiality: All information you supply and recording of your arm movements or judgments about hand location during the experiment will be held in confidence, your name will not appear in any report or publication of the research. Your data will be safely stored password protected computers in our locked laboratory and only research staff will have access to this information. Your personal information will be destroyed after the study has been published or when 5 years have expired since recording. The recorded experimental data (such as arm movements and pupil dilation) will be shared, fully anonymized, in an online academic data repository, in the interest of transparency about this study, as well as for potential use in future studies by other researchers. Confidentiality will be provided to the fullest extent possible by law.

Questions About the Research? If you have questions about the research in general or about your role in the study, please feel free to contact ____ either by telephone at ___, extension ____ or by e-mail (____). This research has been reviewed and approved by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights as a participant in the study, please contact the Sr. Manager & Policy Advisor for the Office of Research Ethics, 5th Floor, York Research Tower, York University (telephone 416-736-5914 or e-mail ore@yorku.ca).

Legal Rights and Signatures:

I________________________, consent to participate in this study conducted by Dr. -___and her research team. I have understood the nature of this project and wish to participate. I am not waiving any of my legal rights by signing this form. My signature below indicates my consent.

Signature______________________ **Date**____________________

Participant

Signature______________________ **Date**____________________

Principal Investigator